FOOD LIMITATION REDUCES BODY LENGTH IN MANTID NYMPHS, *TENODERA SINENSIS* SAUSSURE (MANTODEA: MANTIDAE): IMPLICATIONS FOR FITNESS

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Abstract.—Growth rate and body size have been linked to fitness in the mantid, *Tenodera sinensis* Saussure (Mantodea: Mantidae). We asked how early in the life cycle food level could affect these two parameters. Two laboratory cohorts were offered prey at either high or low density during first and second stadia. These nymphs exhibited significant differences in predation rate, growth rate, and body size, but not in gross growth efficiency. Well-fed nymphs achieved larger body size in a shorter time than poorly fed ones during both their first and second stadia. Because body size of adult females determines maximum fecundity, this response suggests that food level during the early life history of this species can directly affect fitness. Flexibility in body size and rate of development may play an important role in determining distribution and regional persistence of this species in temperate habitats.

Key Words: Body size, fitness, food limitation, growth, Mantidae, Mantodea, *Tenodera sinensis*

For generalist predators such as praying mantids, limited prey availability in nature is common, and can reduce growth, survival, and reproduction (Matsura 1981, Matsura and Marooka 1983, Hurd and Eisenberg 1984, Hurd et al. 1995). The impact of food limitation on growth and development would seem particularly acute for temperate zone mantids, that are faced with a limited growing season in which to complete their life cycles before freezing weather kills the adults.

Tenodera sinensis (Saussure) was introduced into this country in 1896 near Philadelphia, PA (Laurent 1898). It has since become a widespread and abundant mantid in the eastern United States, with a range extending from southern New England through the Carolinas (Rooney et al. 1996). This large-bodied species hatches from contagiously dispersed oothecae early in the spring, leading to dense concentrations of hatchlings when prey levels are low (Eisenberg and Hurd 1990). Low prey availability reduces both rate of development (Hurd and Rathet 1986) and survival (Hurd and Eisenberg 1984) during the early stadia. This is a semelparous, univoltine species which overwinters in the egg stage. Thus, reduced rate of development can retard maturation so that females do not have time to complete seven nymphal stadia, undergo oogenesis, and oviposit before killing frost (Hurd et al. 1995).

One consequence of early food limitation is reduced imago body length, and body length of adult females has been implicated as the limiting factor in egg production. Eisenberg et al. (1981) found that adult females with longer mean body length gained

more mass in the field during oogenesis than those that had lower mean body length at a different site. Mass gain at this time of the life cycle is directly related to number of eggs contained in oothecae (Eisenberg et al. 1981, Hurd 1989). Thus, feeding condition of juvenile mantids can affect fitness (egg production) through body length. We asked how early in the life cycle the effect of food availability on components of fitness might be evident, by raising hatchling *Tenodera sinensis* in the laboratory at two prey abundance levels and recording body lengths at ecdysis and time spent in different stadia.

MATERIALS AND METHODS

Thirty-nine oothecae of *Tenodera sinensis* were collected early in the spring of 1996 from old fields in Rockbridge Co., Va. Four experimental groups of 20 nymphs each were established from individuals that hatched the same day. These groups were fed apterous *Drosophila melanogaster* (Meigen) at two levels and killed by freezing to measure and weigh after either the first or second molt.

Groups A and B were killed after the first molt. Nymphs in group A were fed four flies per day; those in group B were fed one fly per day. Groups C and D were killed after the second molt. Nymphs in group C were fed four flies per day; those in group D were fed one fly per day.

All nymphs were housed individually in 130-ml glass vials having tight lids fitted with fine-mesh brass screening for ventilation, and a hole through which a cotton swab, moistened daily with distilled water, was placed (Hurd and Rathet 1986). All vials were kept in a growth chamber set at 23°C and on a 16:8 (L:D) light cycle.

Body length, from front of head to tip of abdomen, was measured to the nearest 0.1 mm for all killed nymphs after thawing. Dry weight body mass was measured to the nearest 0.1 mg after drying in an oven at 50°C for 24 h. Number of days in a stadium was recorded for each nymph.

Because feeding rate can affect the efficiency with which food is processed by these predators (Hurd 1991), we calculated gross growth efficiency (GGE) for mantid nymphs in the first stadium, for groups A and B:

$$GGE = [(\text{mass gained}) \div (\text{mass of food consumed})] \times 100\%$$

where mass gained was individual mass of a nymph at ecdysis minus an established mean dry mass of 17 nymphs from the original cohort that had been killed, dried, and weighed upon hatching. Mass of food consumed was calculated by multiplying the number of flies eaten during a stadium by the mean dry weight mass measured from 50 flies taken from culture bottles at the beginning of the experiment. GGE could not be calculated for second stadium nymphs in C and D, because we had no baseline for beginning second instars from these two cohorts.

RESULTS

Mantids in both first and second stadia ate more, developed faster, and attained greater mean body length when fed four flies per day than when fed only one per day (Table 1). Group A and C nymphs fed at three to four times the rate of those in groups B and D, respectively.

Group B nymphs took about 50% longer to complete the first stadium than those in group A. The difference in rate of development was even more pronounced during second stadium: group D took nearly three times as long to complete the stadium as group C. In contrast, well-fed nymphs completed both first (A) and second (C) stadia in about the same time.

The percent gain in body length of well-fed nymphs compared to poorly fed nymphs increased from first to second stadium. Well-fed group A nymphs in first stadium attained a mean of 11% greater body length than poorly-fed group B individuals. For nymphs completing second stadium,

Table 1. Mean (±SE) predation rate (flies/day eaten), development time (days in stadium), and body length, for first and second stadium *Tenodera sinensis* nymphs, mean (±SE) percent gross growth efficiency (GGE) for first instars, and results of 2-tailed *t* tests for differences between pairs of groups. Calculation of GGE for first stadium nymphs explained in text. GGE was not significantly different between A and B after table-wide *P* adjustment for multiple comparisons (Rice 1989).

Group	Flies Eaten/Day	Days in Stadium	Body Length (mm)	%GGE
A	2.6 (±0.06)	8.3 (±0.13)	15.2 (±0.11)	30.8 (±0.99)
B	0.9 (±0.01)	12.1 (±0.39)	13.7 (±0.12)	27.4 (±1.24)
A v. B: t_{36} =	−29.83	−9.15	−9.02	−2.14
P =	≪0.001	<0.001	<0.001	0.04 (NS)
C	3.8 (±0.05)	8.2 (±0.14)	20.5 (±0.21)	
D	1.0 (±0.01)	22.8 (±0.74)	16.8 (±0.15)	
C v. D: t_{35} =	54.67	−19.96	13.88	
P =	≪0.001	<0.001	<0.001	

mean body length of group C nymphs was 22% greater than of those in group D. In fact, poorly fed group C nymphs completing second stadium (D) were hardly larger than well-fed group A nymphs completing first stadium.

Feeding level did not significantly affect GGE, though nymphs in group A were slightly more efficient on average than those in B (Table 1).

DISCUSSION

The benefit from increased feeding opportunity in *T. sinensis* nymphs occurred immediately after eclosion, in terms of both size and rate of development. The advantage in body size during first stadium increased during second stadium, indicating that the increased body size of well-fed first instars accumulates as individuals grow, at least through the second stadium. This could explain differences in adult body length (7–10 cm) in a given field population (personal observations). To the extent that body length determines maximum egg production, early feeding clearly can have a significant impact on fitness of females in this species.

Sex cannot be determined in *T. sinensis* until the third stadium, but sex ratio of hatchlings is 50:50 (Moran and Hurd 1994). However, although this means that half of our experimental animals were male, the ef-

fect of body size on male fitness has not yet been demonstrated.

The impact of feeding on development rate was also marked. For well-fed nymphs, the time to complete first and second stadia was about the same (8 days), although nymphs fed a single fly per day took nearly twice as long to complete second stadium as compared to first. Thus, well-fed nymphs took approximately 16 days (total) to complete the first two stadia; poorly fed nymphs, on the other hand, took more than 30 days to do the same thing. Our data suggest that well-fed nymphs could nearly complete four stadia in 30 days. This mantid is an ambush predator, and its nymphs do not move about very much in the field (Rathet and Hurd 1983). Thus, we feel it is unlikely that our nymphs expended significantly less energy in the vials (i.e., have more energy to grow) than they would have in the field.

Hurd (1991) found that %GGE varied with predation rate in first stadium *T. sinensis* nymphs: from 34% for <0.4 flies per day to 57% for 0.8 flies per day, reduced to about 40% for 1.2 flies per day. However, in the present experiment mean %GGE did not significantly differ between groups that ate 0.9 flies/day and those that ate 2.6 flies per day. In fact, %GGE was lower in this experiment than for any group in the earlier study. The design of this experiment was

similar but there may have been a proce-
dural difference, a genetic difference be-
tween these mantid nymphs and those used
in the earlier study, or both that caused the
disparity in results.

The degree of phenotypic flexibility of
body size and rate of development exhib-
ited by this species from the earliest stage
of development has important implications
for its distribution and persistence. Clearly,
its latitudinal distribution will be limited to
habitats of sufficient season length and
feeding opportunity. However, the present
contiguous distribution of this species in the
eastern U.S. (approximately from southern
Pennsylvania to northern Georgia) indicates
a wide tolerance with regard at least to
length of growing season. Because its body
size is flexible, this species should be able
to complete its life cycle under a variety of
food levels. Thus, though early feeding ex-
perience can affect fitness in this species,
flexibility in adult body length may partial-
ly mitigate the predicted shrinkage of re-
gional distribution under global warming
scenarios (Rooney et al. 1996).

The salient features of the life history of
this mantid are shared by many other pre-
dacious arthropods inhabiting temperate
seasonal environments. Our findings that
adult fitness can be influenced by food
availability immediately upon egg hatch
may therefore be more general than for *T.
sinensis*. However, we know of no compre-
hensive studies linking food limitation,
growth rates, body size, and fitness in other
such predators.

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